Behavioural responses of breeding Silver Gulls to tourist traffic

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ABSTRACT

Ground-nesting seabirds are vulnerable to human intrusion which can potentially impair their breeding success. We examined whether tourist traffic on a boardwalk through a Silver Gull *Larus novaehollandiae* breeding colony affected the birds' behaviour sufficiently to potentially decrease reproductive success. Nest density was positively correlated with distance from the boardwalk. Gulls nesting ≤5 m from the boardwalk were more vigilant towards a stationary investigator than those further away. Tourists walking past breeding gulls stimulated a large increase in intra-specific aggression; stopping alongside parents with mobile chicks increased their intra-specific aggression even more. Larger tourist groups (≥3) stimulated more intra-specific aggression than smaller ones. An investigator walking past breeding gulls similarly stimulated an increase in intra-specific aggression, but the investigator's clothing colour, noise emission level and walking speed had no effect on the birds. An ambulatory investigator in another colony infrequently visited by people had a similar effect on gulls' intra-specific aggression, but these birds generally reacted more strongly to human intrusion. Silver Gulls' behavioural responses to tourist traffic could potentially decrease their reproductive success. These responses could be reduced by regulating traffic volume and flow and tourists' group size and behaviour, but the species' public image currently probably mitigates against such regulation occurring.

Key words: Silver Gull, tourist, boardwalk, group size, vigilance, intra-specific aggression, disturbance

Introduction

Gutzwiller and Anderson (1999) characterised human disturbance of wildlife as resulting from the presence of non-predatory humans in the animals' environment, and some animal population declines have been directly attributed to this phenomenon (Flemming *et al*. 1988). Large birds that breed colonially are quite prone to human disturbance, because their aggregations are conspicuous, spatially-fixed entities which consequently often become popular tourist attractions. The susceptibility to human disturbance in such species can be influenced by factors such as the nature of the surrounding habitat, the distance of the colony from human settlement and the physical accessibility of the colony to people (Burger 1981; Burger and Gochfeld 1983; Vos *et al*. 1985).

Colonially-breeding birds that nest on the ground are especially vulnerable to human disturbance effects, particularly when they nest near sites where human recreation occurs (DesGranges and Reed 1981; Burger and Gochfeld 1983). People intruding into such breeding colonies can cause a marked decrease in parental nest attentiveness, a substantial increase in parents' energy expenditure and stress levels and an increase in chicks' fleeing behaviour, changes which can lead to a reduction in breeding success and significant mortality of adults, chicks and embryos (Robert and Ralph 1975; Burger 1981; Anderson 1988; Vermeer *et al.* 1991; Woehler *et al.* 1994; Regel and Pütz 1997; Vleck *et al.* 2000; Weimerskirch *et al.* 2002; Martín *et al.* 2004; Müllner *et al.* 2004). Such disturbance effects have been well documented for ground-nesting, colonial seabirds that are popular tourist attractions, such as many of the penguins (Martin *et al.* 2004; Holmes *et al.* 2005), and for some northern hemisphere gull species (Burger 1981; Gillet *et al.* 1975; Robert and Ralph 1975).

The ground-nesting, colonially-breeding Australasian Silver Gull *Larus novaehollandiae* is very abundant in Australia's coastal cities. At landfill sites and around water supplies, where it can occur in huge numbers and pose pollution and disease transmission threats, it is often considered a pest (Smith *et al.* 1991). It is adept at living semi-commensally with humans (Smith and Carlile 1992) and thus might be expected to be relatively tolerant of human presence. Despite this, it is conceivable that, like many northern hemisphere gulls (Anderson and Keith 1980; Fetterolf 1983; Brown and Morris 1995), it is vulnerable to human disturbance whilst breeding. An understanding of this widespread and apparently robust species' sensitivity to human disturbance could be helpful in managing its populations, particularly in areas with high human population densities. The aim of this study was therefore to determine whether and how breeding Silver Gulls respond to tourist traffic. The principal breeding colony at Point Grant that we studied is unusual in that it is visited daily by hundreds of tourists, who walk right through its heart on a boardwalk elevated ~ 0.5 m off the ground (Fig. 1). It is commonly believed that this colony's long-term persistence (Harris and Bode 1981) indicates that its members readily habituate to human disturbance, but this has not been rigorously investigated. Even if some habituation occurs, it is conceivable that the birds still respond sufficiently to impair their breeding success. Our study examined whether (a) the distribution of nest sites in the colony appeared to be influenced by tourist traffic, (b) breeding gulls exhibited heightened anti-predator behaviour (monitoring and vigilance) in the presence of a human observer on the boardwalk and, if so, whether this was affected by proximity to the observer and (c) pedestrian traffic on the boardwalk affected the gulls' intra-specific aggression levels.

We replicated some of the observations in a second colony 41 km away (Mud Islands), which had a similar gull density but was isolated and had a negligible level of human traffic. These observations allowed us to better calibrate the effect of pedestrian traffic on members of the Point Grant colony, but the colonies differed in several respects and so the Mud Islands observations could not strictly be regarded as a control for those at Point Grant.

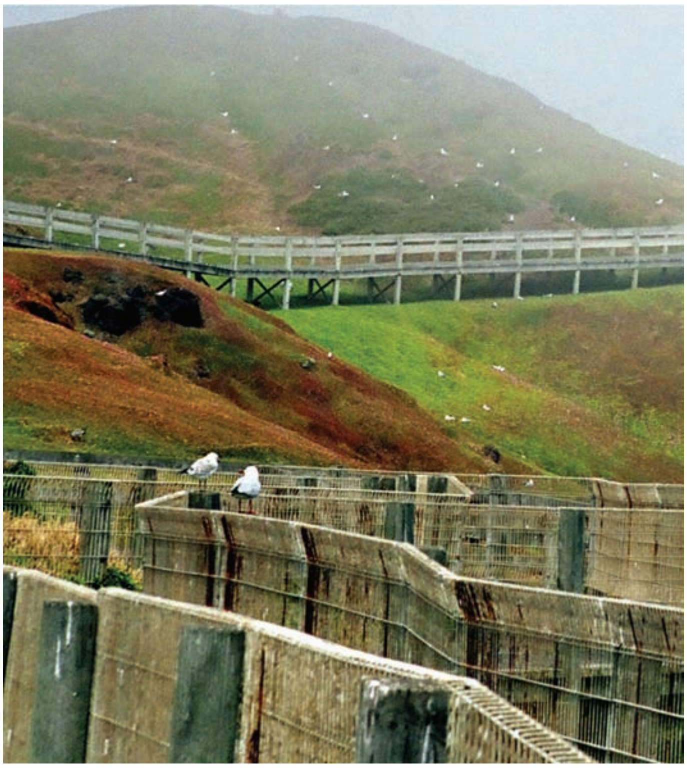

Figure 1. The boardwalk in the Point Grant silver gull colony. The photograph was taken near the end of the breeding season; at the peak of breeding, the grassy area was densely packed with breeding units.

Methods

Study species

Silver Gulls inhabit Australian coastal and inland waters, feed and roost gregariously and breed predominantly on islands in colonies that can comprise thousands of pairs (Wheeler and Watson 1963; Carrick and Murray 1964). They breed from August to February in southern Australia, colony numbers peaking from September to December. They usually nest on the ground in small scrapes lined with feathers and vegetation. Most nests are in the open, but some are under bushes, in thickets and in the entrances of abandoned penguin burrows. Pairs of adults initiate 1-3 breeding attempts per season and breeding is relatively synchronised within a colony, with 80% of adults laying their clutches within a 10-14 day period. The usual 1 to 3-egg clutch is laid within a few days of nest completion and the incubation period lasts 19-26 days (Wheeler and Watson 1963). After hatching, the semi-precocial chicks either leave the nest and hide in nearby vegetation or remain at the nest site for up to one week. They leave the colony after 3.5-4 weeks, but are fed by their parents for up to six weeks. Breeding typically commences when birds are about 2 years old. Silver Gulls' diet includes fish, terrestrial and marine arthropods, human refuse and even fruit. They can transmit human enteric pathogens and cause air strikes with aircraft (van Tets 1969 a, b).

Study sites

Colonies were studied from September to January in 2006-2007 and 2007-2008. One colony occupied 0.044 km^2 of Point Grant (38º 31' S, 145º 07' E) on the south-western extremity of Phillip Island, Western Port Bay, Victoria and was visited daily by large numbers of tourists in spring and summer. Ironically, Silver Gulls started breeding on Point Grant a few years after an elevated boardwalk was constructed in the late 1970s for tourists to view a seal colony and nearby geological formations. It was installed to prevent soil erosion and conserve the vegetation (Harris and Bode 1981). It is fenced on both sides, approximately 2m wide and 695m long and passes through the centre of the colony, some birds actually nesting below or immediately adjacent to it (Fig 1). Gulls sometimes perch on the boardwalk's walls, but infrequently when tourists are nearby. The landward area immediately adjacent to the colony contains a road that carries vehicular traffic during the day. The other colony that we investigated was on Mud Islands (38º 16' S, 144º 46' E) in Port Phillip Bay, Victoria. The three low-lying islands comprising this group have a combined area of ~0.6 km^2. They are only accessible by shallow-hulled and small boats and so human visitors are few; thus it provided a strong contrast with Point Grant in terms of human disturbance. Observations on Mud Islands were restricted to fine, still days due to the difficult access by sea. The ~0.25 km^2 gull colony occupies most of the outer perimeter of the islands' main land mass and is accessible on foot, but there is no boardwalk or formed track. As far as we know, there is no Victorian Silver Gull colony that has both a low pedestrian traffic volume and a boardwalk, which would make an ideal comparison with Point Grant in terms of accounting for any effects of the presence of a boardwalk *per se*.

Procedures

Nest site dispersion at Point Grant

Twenty-nine 20 m long transects ≥ 10 m apart were surveyed in the Point Grant colony to document nest dispersion and ascertain whether nest density was correlated with any of three habitat variables. Transects originated from both sides of the boardwalk, but as it did not follow a straight line, siting of transects was arranged so as to avoid intersection. At 1 m intervals along each transect we recorded the number of nests that intersected, or were ≤ 1m from the transect, the type of vegetation present (none, herbaceous shrub or grass) and topography (ground sloping i.e. gradient ≥ 0.3 or level i.e. gradient = 0). Transects were surveyed four times during the 2007-2008 breeding season at intervals of ~ 4 weeks and mean numbers of nests per sampling point were then examined as a function of distance from the boardwalk, vegetation present and topography.

Response of gulls to a stationary investigator at Point Grant

Responses of breeding gulls at Point Grant to the presence of an investigator on the boardwalk were recorded between 0730 and 0830 AEDT, before any tourists arrived, on 52 days from October to December in 2006 and 2007. The first observation each day was made at a random distance within 100 m of the boardwalk's entrance; subsequent observations were made at ~100 m intervals from that location. At each observation 'station', the first breeding gull observed became the focal bird for study, its behaviour being recorded for 2 min by instantaneous sampling (Martin and Bateson 2007) at 4-sec intervals using an audio cassette recorder. At each time interval, the occurrence of behaviour oriented towards the investigator (investigator-oriented behaviour, IOB) or towards other aspects of the bird's environment (environment-oriented behaviour, EOB) was recorded. IOB involved (a) visual fixation of the investigator; this was clearly detectable from the bird's head orientation and was assumed to be vigilance and (b) attacking or mobbing the investigator. EOB encompassed visual scanning of the surrounding environment and aggressive posturing towards, or attacks on, con-specifics or members of other bird species. We also recorded (a) distance (> or ≤ 5 m) of the focal bird from the investigator, using a Bushnell© 450 laser range finder, (b) breeding phase it had attained (incubation/brooding or accompanying mobile chicks) and (c) number of con-specifics within 1m of it; this measurement was treated as a co-variate in analysis and was included to control for variation in the number of gulls present during an observation. Parents of juvenile-plumaged chicks were excluded from these observations, because juveniles require less attention and protection than younger chicks.

Intra-specific aggression elicited by tourists at Point Grant

The incidence of intra-specific aggression stimulated by the presence of visiting tourists was measured from 1000–1100 and 1430–1530 AEDT on 26 days from November to January in 2006 and 2007 at Point Grant. Focal groups of gulls at 15 locations throughout the colony were observed from the boardwalk from a distance of ≥ 25 m with 8 X 40 binoculars. Focal group size (i.e. number of adult and young gulls) was 2–10 and was chosen haphazardly, provided that all focal gulls could be observed simultaneously. The incidence of intra-specific aggression involving focal gulls was recorded on a cassette recorder before (approaching tourist(s) within 15-20 m, S1), during (tourist(s) alongside, S2) and after (retreating tourist(s) 15–20 m away, S3) tourists walked past them on the boardwalk. Each of these stages of tourist progress (S1-S3) usually lasted ~30 sec. Intra-specific aggressive behaviour was categorised during preliminary observations and resembled that of other *Larus* spp. (Carrick and Murray 1964; Higgins and Davies 1996).

The frequency of intra-specific aggression involving focal gulls was analysed as a function of (a) tourist group size (≤ 2 and ≥ 3), (b) tourists' clothing conspicuousness (light, dark, dull or bright, based on the most common shade of garment worn on the upper half of the body by group members), (c) whether tourists stopped opposite the focal birds and (d) dominant breeding phase of the focal gulls. Ultraviolet reflectance is important in prey and predator detection by birds (Hart 2001; Ödeen and Håstad 2003) and the clothing conspicuousness categories took this into account. The categories 'light' and 'dark' included white and black, respectively, but also light and dark shades of primary and secondary colours (e.g. dark green, navy blue etc.). The 'dull' category included khaki, brown and grey and the 'bright' category encompassed shades of red, yellow, orange and many fluorescent fabrics.

Intra-specific aggression elicited by an ambulatory investigator at Point Grant and Mud Islands

We investigated the eliciting of intra-specific aggression in breeding gulls by a mobile investigator in a series of comparative observations made at Point Grant and Mud Islands. Focal groups of 2–10 adult and young gulls were selected 'haphazardly' and an investigator walked past them at a distance of 1–3 m on the boardwalk (Point Grant) or along the beach (Mud Islands) in a stereotyped manner. Whilst these were not exactly equivalent intrusions because the Point Grant birds near the boardwalk were mostly more centrally located in the colony, accessing and walking past central Mud Islands birds would probably have caused an ethically unacceptable level of destructive disturbance. To improve independence of the data, we observed focal gulls spread throughout the two colonies at 18 and 17 locations, respectively, and avoided re-sampling gulls at particular locations. We again employed the approaching-alongside-retreating paradigm, with each stage lasting ~ 30 sec.

In the Point Grant observations we determined whether three potentially disturbing facets of the passer-by's behaviour and appearance affected the frequency of gulls' intra-specific aggression:

(1) estimated velocity - categorised as 'slow' ~1-2 or 'regular' 3-4 km/hr

(2) noise emission level- categorised as 'silent' or 'noisy' and achieved by the passer-by continuously playing a pre-recorded audio file of people talking at a sound volume comparable to that which actual conversing passers-by would generate.

(3) clothing conspicuousness – categorised as 'black' or 'white' to provide ultra-violet contrast.

The walk-past events were conducted in batches termed 'trials'. A trial involved an observer walking past a focal gull group six times at intervals of 30-60 sec. Each category of walking velocity, noise emission level and clothing colour (six categories in all) was presented in one of these walk-past events in a randomized order, whilst the other aspects of passer-by behaviour and appearance were held constant e.g. walking velocity (regular) and noise emission level (silent) were held constant across the clothing colour (i.e. black and the white) walk-past events. However, the influence of each facet of passer-by behaviour and appearance was analysed separately.

In the Mud Islands observations, gulls were much less used to human presence and reacted more dynamically to it. Consequently only the effect of walk-past stage (S1-3) could be analysed and walk-past events had to be conducted somewhat differently to permit accurate recording of intra-specific aggression. Thus walk-past stages lasted 2 min (rather than 30 sec) and the walker's velocity was always ~3-4 km/hr. The approach stage was preceded by a 10 min 'settling-down' period, the alongside stage was defined by the walker being within ~20 m of the focal gulls and the retreat stage as when the walker had progressed ~30-40 m past the focal gulls. Focal gulls were again effectively selected haphazardly. However, because all Mud Islands gulls typically took flight as the walker approached and individuals could consequently not be identified and monitored throughout the walk-past event, a ~2 m^2 area containing at least one active nest was selected as the focus for recording and the behaviour of the focal gulls in this area was recorded. In this set of observations, the unavoidable disparities in methods used in the two colonies meant that the Mud Islands colony was not a perfect control, but it still provided an interesting comparison with the high-traffic Point Grant colony.

Data analysis

Nest site dispersion

The number of nests in each 1 m interval from the boardwalk was summed for all transects and all surveys and the overall mean number of nests for each distance interval was calculated. Vegetation and slope categories did not change over the four surveys; they were assigned numerical values and the mean value was calculated for each 1m interval from the boardwalk. A multiple linear regression and tests for partial regression slopes were performed in Systat 10 (Wilkinson 2000) using distance from the boardwalk, vegetation type and slope of the terrain as predictor variables and the mean number of nests (log-transformed to increase linearity Quinn and Keough 2002) as the response variable.

Responses to an investigator and tourists

IOB, EOB and intra-specific aggression data were ln(x)-transformed, but not standardized. They were analysed with distance-based multivariate analysis for a linear model (DISTLM) v5 (Anderson 2004) and permutational multivariate analysis of variance (PERMANOVA), in which a multivariate analysis tested the data for significance using a distance matrix under permutation to produce a P value from a pseudo F value (McArdle and Anderson 2001; Anderson 2005). These analyses are similar and the equivalent of a semi-parametric Analysis of Variance (ANOVA) for unbalanced and balanced designs, respectively (Anderson 2001). Advantages of these tests for analysing our data were that they could accommodate the many zero values obtained and they controlled for non-independence of the values obtained at each stage of a walk-past event (M. Anderson, personal communication). With the exception of the ambulatory investigator trials, DISTLM performed a permutational test, based on Bray-Curtis dissimilarity distances (Anderson 2004). XMATRIX was used to produce design matrices to be used in DISTLM corresponding to factors and interaction term(s) in ANOVA designs (Anderson 2003). However, as the data from the ambulatory investigator trials at Point Grant and Mud Islands contained factors with the same number of observations (i.e. there was a balanced design), a PERMANOVA was performed without the aid of XMATRIX on these data. For each analysis, permutations of residuals under a full model were used to calculate F and P values in DISTLM (Anderson 2004). The full model included the matrices for each of the factors, the interaction term(s) and any covariates (Anderson 2003). For the ambulatory investigator and tourist trials, p*ost-hoc* pair-wise comparisons were performed among the values for the three sampling times (before, during and after the passage of an investigator or tourist group) in DISTLM and PERMANOVA. In accordance with Manly's (1997) recommendations, 999 permutations were used to obtain an α-level of 0.05. Results are presented as means ± standard error.

Intra-specific aggression frequencies were divided by the number of gulls in the focal group to control for disparities stemming purely from focal group size variation; they are therefore presented throughout as the number of aggressive events per focal gull per observation, but 'per observation' is routinely omitted for brevity. The mean number of gulls per focal group did not differ between the Point Grant and Mud Islands colonies (Point Grant 4.49 ± 0.09, Mud Islands 4.45 ± 0.14; $F_{1,378} = 0.054$, $P = 0.817$). As the ratio of adult: immature gulls in a focal group could potentially also have influenced intra-specific aggression levels, the proportion of adults in the group was included as a covariate in all analyses of this behaviour. In examining intra-specific aggression stimulated by visiting tourists, we obtained and separately analysed three distinct, non-overlapping data sets for different breeding phases, namely incubation, chick-rearing and incubation-plus-chick-rearing combined. In data analyses for the first two phases, the factors examined were tourists' walk-past stage, clothing colour conspicuousness and stopping behaviour (absolute tourist group size was included as a covariate). In the analysis of the combined incubation-plus-chick-rearing data set, the factors were just tourists' walk-past stage and group size (categorised as 'small' 1-2, or large ≥ 3). Some combining of clothing colour categories was necessary in one analysis.

Results

Nest site dispersion

At Point Grant, the mean number of nests occurring at a survey point was not influenced by type of vegetation present (no vegetation 1.3 ± 0.1, herbaceous shrub 0.6 ± 0.1 and grass 0.8 ± 0.1; $t_{16} = -1.03$, $P = 0.321$) or the slope of the terrain (sloping 0.8 ± 0.1, level 0.9 ± 0.1; $t_{16} = -0.90$, $P = 0.380$). However, it was positively related to distance from the boardwalk ($t_{16} = 4.40$, $P < 0.001$; $R^2 = 0.557$) (Fig. 2). At the greatest distance from the boardwalk that we surveyed (20 m), the mean number of nests (12.5) was 5 X the smallest mean (2.3), which occurred at 3 m.

Response to a stationary investigator

Point Grant gulls close to and farther away from the boardwalk on which the investigator stood spent similar proportions of time in EOB (37.2 ± 2.0% and 43.1 ± 2.2%, respectively; $F_{1, 274} = 2.27$, $P = 0.107$). However, gulls nesting within 5 m of the structure exhibited more IOB (52.1 ± 2.3% of observation time) than those nesting >5 m from it (20.2 ± 2.05%; $F_{1, 274} = 50.80$, $P = 0.001$). Gulls nesting close to the boardwalk responded to the investigator in several ways (e.g. taking flight, swooping), but the most frequent response was to remain near the nest and visually fixate the investigator (49% of occasions), often for most of the observation period. In contrast, gulls >5 m from the boardwalk often did not to respond overtly to the investigator, continuing to sleep, preen or feed their chicks (43% of occasions). The only effect of breeding phase on response to the investigator was that gulls with older chicks devoted proportionately more time to EOB than those incubating eggs or brooding hatchlings (48.1 ± 2.2% versus 34.8 ± 1.9% of observation time; $F_{1, 274} = 3.58$, $P = 0.028$).

Intra-specific aggression in response to tourists

Whether gulls were incubating/brooding or caring for mobile chicks, the frequency of their intra-specific aggressive behaviour was affected by tourists walking past them. Thus for incubating/brooding gulls, the mean number of intra-specific aggressive events per focal gull per observation increased six-fold from the tourists' approach to whilst they were alongside, before decreasing again by a factor of 4.7 during their retreat (*post hoc* pair-wise comparisons: approach = retreat; approach and retreat both < alongside). The corresponding changes for adults with mobile chicks were an eight-fold increase and a four-fold decrease (*post hoc* comparisons: approach = retreat; approach and retreat both < alongside) (Table 1). Tourists stopping alongside gulls that were caring for mobile chicks, but not incubating or brooding, significantly increased the gulls' aggression (Table 1). The mean increase in intra-specific aggression between the approach and alongside stages of a tourist walk-past at this phase of breeding was 11-fold when tourists stopped, but only four-fold when they did not. Apparent conspicuousness of the tourists' clothing did not significantly influence the frequency of intra-specific aggressive acts per focal bird at either breeding phase (Table 1). However, tourist groups with 3 or more members stimulated a significantly greater increase (seven-fold) in intra-specific aggressive acts per gull between the approach and alongside stages of a walk-past than groups with <3 members (three-fold increase) (Fig. 3; test statistics in figure legend).

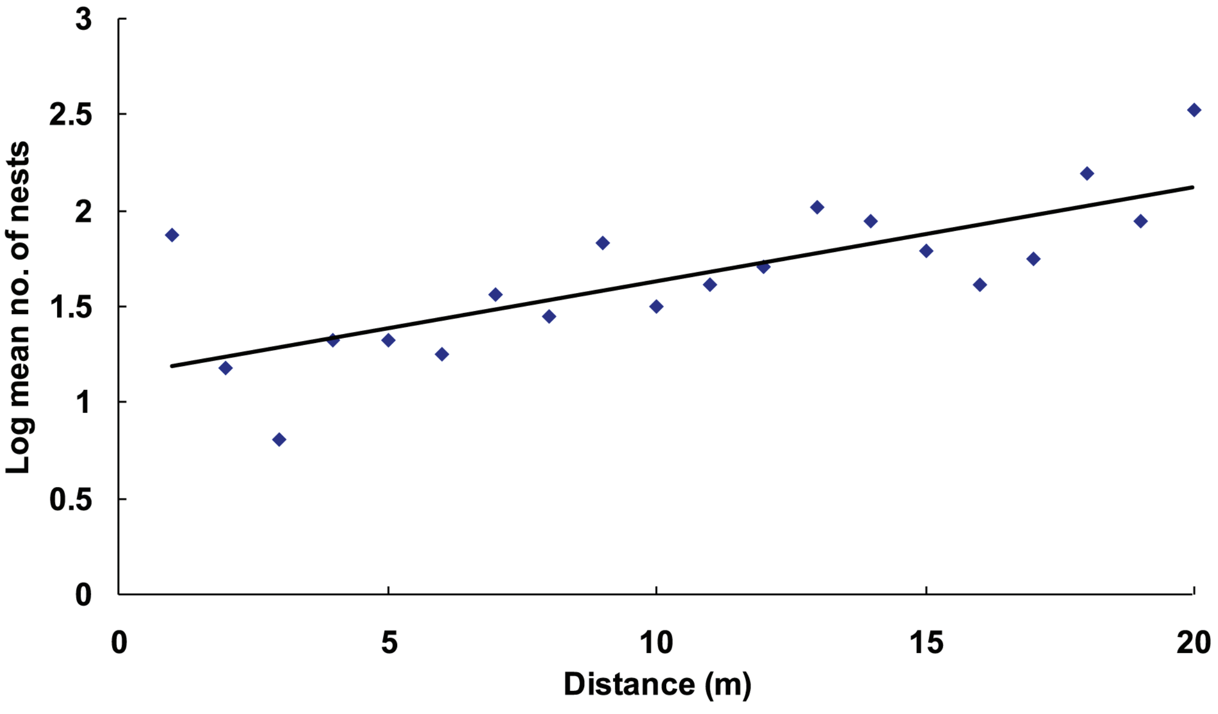

Figure 2. Log mean number of nests per survey point at Point Grant as a function of distance from the boardwalk (1-20 m).

Table 1. Outcome of a DISTLM analysis examining the effect of walk-past stage (S1-3), clothing conspicuousness (dark, bright and light) and behaviour (stop, not stop) of tourists on Silver Gull intra-specific aggression. Number of observations (N) is the number of walk-past events. Significant F and P values shown in bold. d. f. = degrees of freedom.

Breeding phase	Interaction/Factor	d. f.	F	P	Factor alternatives	Mean ± S. E.
Incubation brooding (N = 95)	Stage × Conspicuousness × Behaviour	4	0.14	0.992		
	Stage × Conspicuousness	4	0.4	0.848		
	Stage × Behaviour	2	0.59	0.561		
	Conspicuousness´ Behaviour	2	0.09	0.97		
	Stage	2	**15.55**	**0.001**	S1	0.07± 0.03
					S2	0.42 ± 0.09
					S3	0.09 ± 0.03
	Conspicuousness	2	2.65	0.059	Dark S1	0.10 ± 0.04
					S2	0.54 ± 0.20
					S3	0.11 ± 0.05
					Bright S1	0.10 ± 0.01
					S2	0.75 ± 0.14
					S3	0.03 ± 0.02
					Light S1	0.10 ± 0.07
					S2	0.37 ± 0.09
					S3	0.11 ± 0.05
	Behaviour	1	2.65	0.096	Stop S1	0.10 ± 0.04
					S2	0.55 ± 0.14
					S3	0.10 ± 0.04
					Not stop S1	0.02 ± 0.02
					S2	0.38 ± 0.07
					S3	0.06 ± 0.04
	Covariate	2				
	Residual	265				
Chick-rearing (N = 292)	Stage × Conspicuousness × Behaviour	6	1.21	0.322		
	Stage × Conspicuousness	6	0.4	0.918		
	Stage × Behaviour	2	**6.9**	**0.002**		
	Conspicuousness × Behaviour	3	0.84	0.478		
	Stage	2	**13.42**	**0.001**	S1	0.02 ± 0.01
					S2	0.16 ± 0.03
					S3	0.04 ± 0.01
	Conspicuousness	3	2.28	0.067	Dark S1	0.01 ± 0.01
					S2	0.13 ± 0.04
					S3	0.23 ± 0.02
					Bright S1	0.04 ± 0.02
					S2	0.27 ± 0.07
					S3	0.05 ± 0.02
					Light S1	0.01 ± 0.01
					S2	0.04 ± 0.02
					S3	0.02 ± 0.02
					Dull S1	0.03 ± 0.03
					S2	0.13 ± 0.05
					S3	0.03 ± 0.02
	Behaviour	1	0.82	0.4	Stop S1	0.02 ± 0.01
					S2	0.22 ± 0.04
					S3	0.03 ± 0.01
					Not stop S1	0.03 ± 0.01
					S2	0.10 ± 0.04
					S3	0.05 ± 0.02
	Covariate	2				
	Residual	850				

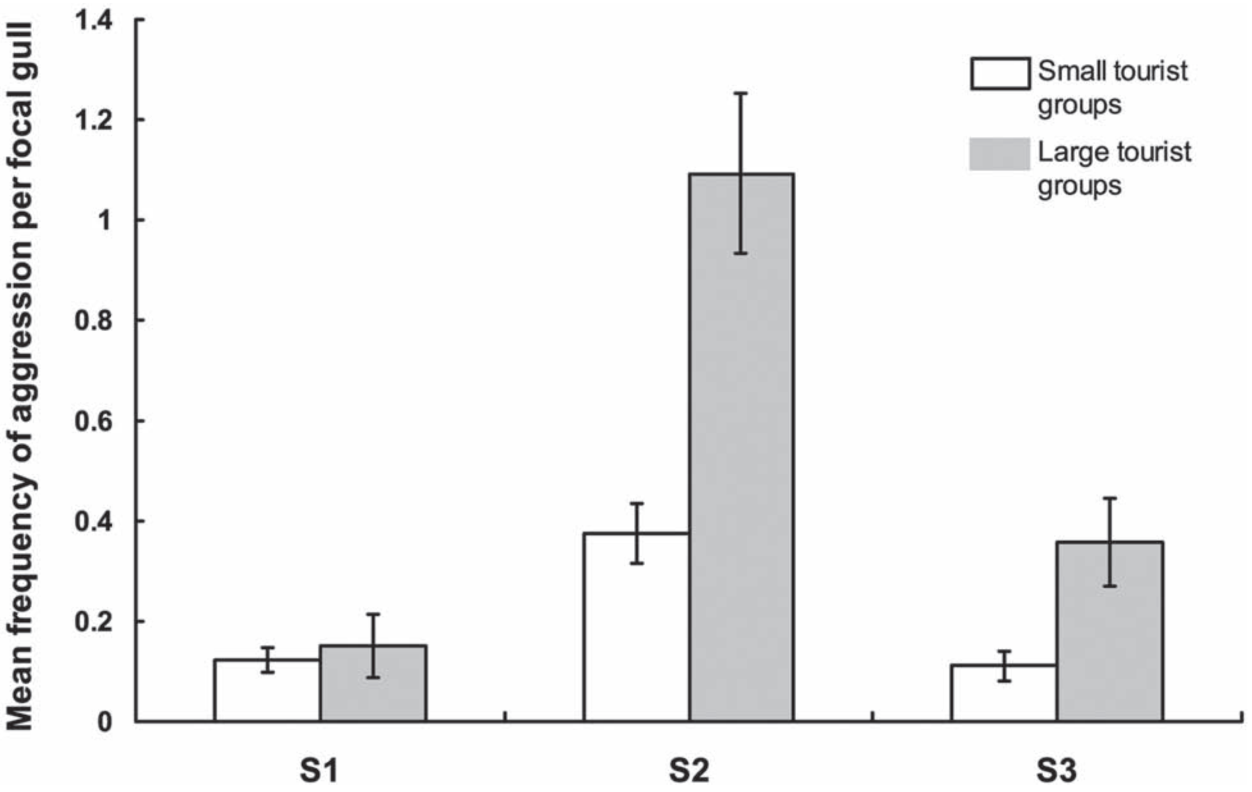

Figure 3. Mean (± standard error) frequency of focal silver gulls' involvement in intra-specific aggressive interactions (per observation) when tourists were approaching (S1), alongside (S2) and retreating from them (S3) during a walk-past event at Point Grant. Small tourists groups (< 3 members) in white, large groups (≥ 3 members) shaded. DISTLM outcome: Stage (S1-3) X tourist group size interaction, $F_2 = 5.27$, $P = 0.006$; main effects for Stage, $F_2 = 37.12$, $P = 0.001$ and Tourist group size, $F_1 = 5.39$, $P = 0.024$.

Intra-specific aggression in response to an ambulatory investigator

At Point Grant, the mean frequency of intra-specific aggressive acts per focal gull increased in response to a single investigator walking past in two of the three basic versions of walk-past employed (Table 2). From the approach to the alongside stage (S1-S2), the mean frequency increased two-fold in the clothing colour version and by a factor of 2.25 in the velocity version. *Post hoc* pair-wise comparisons indicated that these increases were significant, but that there was not a return to pre-disturbance levels in the retreat stage. In the noise emission level version of the walk-past, mean frequencies did not vary significantly among the three stages. However, although there were thus some walk-past effects on intra-specific aggression, they were not significantly influenced by any of the investigator attributes (clothing colour, velocity or noise emission level) that we measured *per se*, as evidenced by the lack of significant main effects or interaction terms for any of these variables in the analyses summarised in Table 2.

The mean frequency of intra-specific aggression per focal gull also changed significantly in response to an investigator walking past in the Mud Islands colony ($F_{2, 161} = 7.33$, $P = 0.001$) (Fig. 4). There was a nearly two-fold increase between the approach and alongside stages ($P < 0.05$), but no change thereafter ($P > 0.05$). Mud Islands gulls spent, on average, 36% of the alongside stage of an investigator walk-past in flight above the colony and the intruder.

Discussion

Nest dispersion in the Point Grant colony

At Point Grant, the mean number of active nests at a survey point increased as a function of distance from the boardwalk. Vegetation cover and topography did not influence nest dispersion, but because of its height and opaque walls, the boardwalk may have reduced the efficiency of surveillance for predators of gulls nesting close to it to a minor extent. However, probably the strongest reason for actively avoiding nesting near the structure was avoidance of human disturbance. Similar avoidance of human traffic has been observed in colonial Adélie Penguins *Pygoscelis adeliae* (Woehler *et al.* 1994). Gulls nesting close to the boardwalk spent 30% more time visually monitoring an investigator standing on it than did birds nesting further away. The allocation by these gulls of 52% of the time that people were in close proximity to monitoring them had the potential to significantly reduce the time that could be spent on important maintenance and breeding activities, particularly as there was heavy pedestrian traffic on the boardwalk on most days.

Nonetheless some gulls nested very close to the boardwalk. This may have happened by default, with later-arriving (and possibly less-experienced) birds being forced to nest in an inferior breeding location with high human disturbance levels because all less-disturbed locations were already occupied. Ottaway *et al.* (1988) showed in some other Silver Gull

Table 2. Outcome of a PERMANOVA examining the effect of investigator's clothing colour (white, black), velocity (slow, regular speed) and noise emission level (noisy, silent) on the intra-specific aggression of Silver Gulls during walk-past events. N is number of walk-past events. Means are mean frequencies of involvement in intra-specific aggressive interactions per focal gull (per observation). Stages of the walk-past were S1 approach, S2 alongside and S3 retreat. Significant results in bold. d. f. = degrees of freedom.

Interaction/Factor	N	d. f.	F	P	Factor alternatives	Mean ± S. E.
Colour X Stage	80	2	0.89	0.412		
Walk-past Stage		2	**3.14**	**0.032**	S1	0.08 ± 0.03
					S2	0.16 ± 0.04
					S3	0.1 ± 0.03
Colour		1	0.33	0.605	White S1	0.08 ± 0.04
					S2	0.16 ± 0.05
					S3	0.06 ± 0.03
					Black S1	0.09 ± 0.04
					S2	0.17 ± 0.06
					S3	0.14 ± 0.06
Covariate		1				
Residual		233				
Velocity X Stage	80	2	0.22	0.847		
Walk-past Stage		2	**6.53**	**0.002**	S1	0.08 ± 0.04
					S2	0.18 ± 0.04
					S3	0.12 ± 0.03
Velocity		1	0.49	0.485	Regular S1	0.06 ± 0.05
					S2	0.17 ± 0.05
					S3	0.12 ± 0.05
					Slow S1	0.11 ± 0.05
					S2	0.19 ± 0.06
					S3	0.12 ± 0.04
Covariate		1				
Residual		233				
Noise level X Stage	56	2	0.51	0.631		
Walk-past Stage		2	0.75	0.487	S1	0.04 ± 0.02
					S2	0.06 ± 0.03
					S3	0.11 ± 0.04
Noise level		1	0.05	0.921	Noisy S1	0.02 ± 0.01
					S2	0.06 ± 0.04
					S3	0.12 ± 0.05
					Silent S1	0.06 ± 0.04
					S2	0.06 ± 0.03
					S3	0.11 ± 0.07
Covariate		1				
Residual		161				

colonies that it was the older (> 4 years) adults that occupied the best breeding sites, whose vegetation and topography minimized intra-specific aggression and exposure to extreme weather. Mills (1973) also found that older Red-billed Gull *L. novaehollandiae scopulinus* females tended to breed earlier and secure the 'safest' territories. However, it is also possible that there was a trade-off between the disturbance-related disadvantage of nesting near the boardwalk and two benefits. The boardwalk's structure provided some protection from adverse weather in a very exposed site, albeit probably quite limited. More significantly, despite signage discouraging the practice, tourists intentionally and/or accidentally provided gulls nesting near the boardwalk with some supplementary food. The relative importance of disturbance and supplementary food in determining nesting dispersion could be explored by quantifying the supplementation level and documenting the spatial occupancy pattern of the colony at the start of the breeding season. It is unlikely that the occurrence of food supplementation enhanced the level of intra-specific aggression triggered by tourist approach at Point Grant, because un-provisioned Mud Islands and provisioned Point Grant birds exhibited similar increases in this behaviour in response to an investigator's approach.

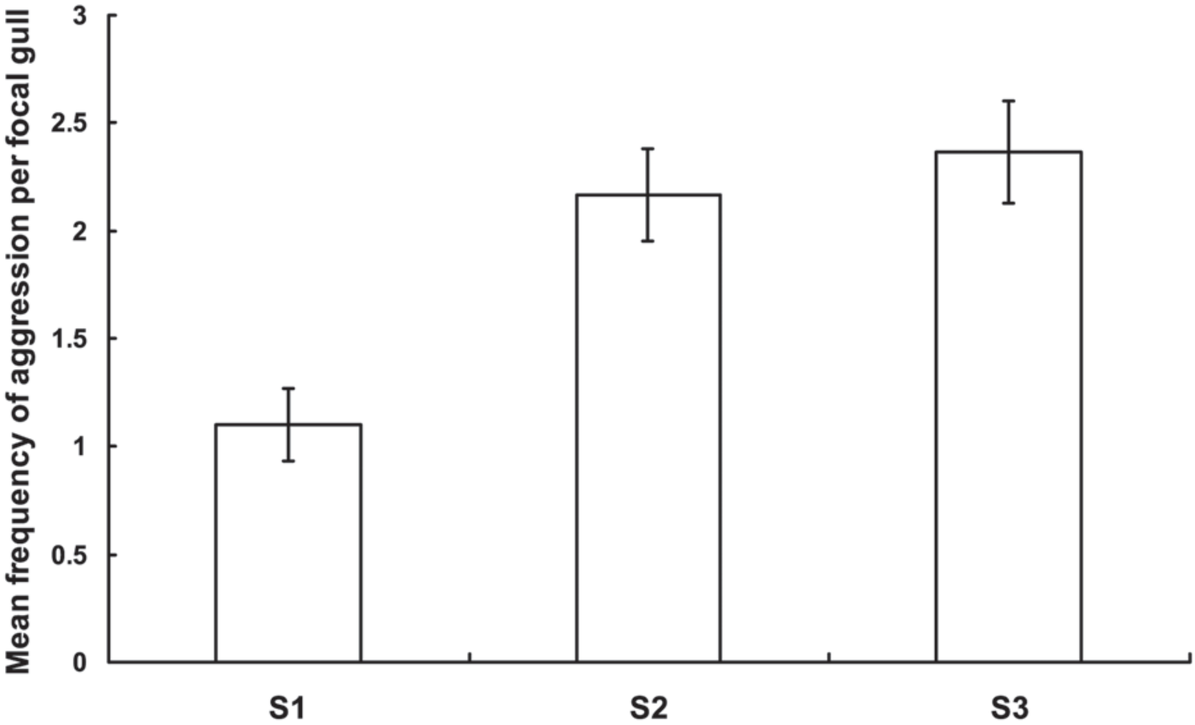

Figure 4. Mean (± standard error) frequency of focal silver gulls' involvement in intra-specific aggressive interactions per observation when an investigator was approaching (S1), alongside (S2) and retreating from them (S3) during a walk-past event at Mud Islands.

Response to a stationary investigator

Gulls nesting close to an investigator standing on the boardwalk exhibited significantly more IOB, but not EOB, than gulls nesting >5m from him/her. IOB was mainly strongly-focused visual monitoring of the intruder. We interpreted EOB as being mainly more generalised anti-predator surveillance and therefore of equal importance to birds close to and further from the boardwalk in view of the intermittent presence of predatory ravens *Corvus* spp. and raptors throughout the colony.

As tourist traffic on the boardwalk was heavy on most days, it is pertinent to consider whether there were likely to be negative consequences of this heightened IOB for gulls nesting close to the boardwalk. The resultant reduction in the time allocation to other critical behaviours alluded to above is likely to be less dramatic at the incubation/brooding stage, as simultaneous performance of these 'static' behaviours and IOB is more feasible than combining IOB and caring for mobile chicks. However, studies of gulls and other birds have shown that disruption of the normal breeding time-activity budget can result in poorer body condition and chronic stress in parents (Siegel 1980; Sapolsky *et al.* 2000; Vleck *et al.* 2000; Holmes *et al.* 2005). Offspring development can be negatively affected too through transference of high concentrations of corticosterone from the maternal circulation to the egg yolk (Liu *et al.* 2000; Kitaysky *et al.* 2003; Hayward and Wingfield 2004; Rubolini *et al.* 2005). Gulls nesting close to the boardwalk frequently temporarily abandoned their nest when approached by the investigator, leaving the eggs or hatchlings exposed to radiant heat which could cause egg addling or nestling hyperthermia (Hayward and Wingfield 2004). Even frequent, short interruptions of incubation can impair hatching success (Tinbergen and Williams 2002) and cause embryo and chick mortality through cold stress, predation and cannibalism (Hunt and Hunt 1975; Kury and Gochfeld 1975; Burger and Gochfeld 1981).

Many breeding birds treat human intruders as predators, presumably because they share many pertinent stimulus properties with them (Blumstein *et al.* 2003; Beale and Monaghan 2004). It has been predicted that the intensity of anti-predator behaviour directed at a human intruder should reflect the perceived risk posed to the parent and young and the level of investment in, and survival probability of, the offspring being defended (Ydenberg and Dill 1986; Montgomerie and Weatherhead 1988). The responses of Silver Gulls to a stationary investigator did not completely match this prediction. Parents with older young with a higher replacement value and greater survival probability certainly exhibited more EOB in the presence of an investigator than parents with eggs or hatchlings. However, only IOB was sensitive to the proximity of a human intruder and the IOB levels of parents with older and younger offspring were indistinguishable.

Stimulation of intra-specific aggression by pedestrian traffic

Point Grant and Mud Islands gulls reacted to an ambulatory pedestrian by exhibiting an approximately two-fold increase in intra-specific aggression. This intriguing response was generated somewhat differently in the two colonies. At Point Grant, approached gulls ran or flew from their territory into neighbouring ones, stimulating attack by the resident birds; however, they soon returned to their own territory, so the effect was quite short-lived. In contrast, when approached by a person, all Mud Islands focal gulls took to the air and did not return to their territories until the human intruder was a considerable distance past their nest. In the relatively protracted interval for which territories were vacated, other gulls opportunistically invaded them and it took some time for the returning residents to oust them. We could not determine whether the intruders were other breeding adults or non-breeding adults which are thought to occasionally enter the colony (Carrick *et al.* 1957; Murray and Carrick 1964; Wooller and Dunlop 1979). The more extreme response of the Mud Islands gulls to pedestrian traffic presumably reflected their far less frequent exposure to human intrusion (Burger and Gochfeld 1983).

The only specific facets of tourists' appearance and behaviour that we measured which influenced the intra-specific aggression of Point Grant Silver Gulls were group size and stopping alongside the focal birds. The gulls apparently perceived larger groups of tourists as more threatening and were thus more likely to flee, consequently invading more neighbouring territories and stimulating more aggressive defence by their owners. That perceived risk of predation is influenced by predator numbers has also been described in some waterbirds, currawongs *Strepera* spp. and parrots (Burger and Gochfeld 1998; Frid and Dill 2002; Geist *et al.* 2005). Stopping alongside gulls may have been particularly threatening because it resembles active, focused predatory behaviour; a predator that stops near potential prey is more likely to attack them than one which walks or runs past apparently ignoring them and many prey clearly recognise this distinction (Frid and Dill 2002). Most tourists who stopped adjacent to the gulls turned to look at them; the increased facial exposure might also have increased the birds' perception of predation risk, as has been suggested for prey species such as the Black Iguana *Ctenosaura similis* (Burger and Gochfeld 1993). Stopping by tourists only increased intra-specific aggression when the focal gulls were parents attending older chicks; this probably reflected the greater mobility of older chicks, which were also likely to flee and so invade neighbouring territories. Although tourists' clothing colour did not affect the frequency of intra-specific aggression in Point Grant gulls, it is known to affect approachability in some bird species, although the response is fairly species-specific and apparently influenced by the species' own plumage colour (Gutzwiller and Marcum 1997). Moreover, we acknowledge that our categorization of clothing colour was fairly 'coarse-grained'. It was interesting that strolling slowly, which prolonged the tourists' proximity to focal gulls, did not stimulate more intra-specific aggression than walking at a brisker pace.

There were several possible negative impacts of the increase in Silver Gull intra-specific aggression caused by tourist traffic. Injury and death of chicks increases dramatically as a result of human intrusion in several gull species (Gillet *et al.* 1975; Robert and Ralph 1975; Anderson and Keith 1980; Burger 1981; Fetterolf 1983; Brown and Morris 1995) and we observed territorial adult Silver Gulls responding very violently to chicks displaced by human proximity in both colonies. Aggressive behaviour is also energetically costly to perform in gulls, as suggested by the negative correlation between body mass and the frequency of display behaviour in juvenile Black-headed Gulls *L. ridibundus* (Ros *et al.* 1997). Meeting the energy costs of an increase in intra-specific aggression probably often requires a compensatory decrease in other areas of the daily energy budget, which may be disadvantageous. Aggressive behaviour in birds is strongly regulated by testosterone (Wingfield *et al.* 1990), but a persistently elevated blood testosterone concentration can reduce parental care behaviour, increase tissue damage resulting from high levels of free radicals in the bloodstream and potentially decrease immune competence (Ros *et al.* 1997; Royle *et al.* 2001). Therefore it is likely that a high and consistent daily level of tourist traffic, such as that at Point Grant, would have some fitness-reducing effects on the birds through elevating the frequency of intra-specific aggression. Moreover, these effects may cascade through nearby colonies of other species; as we traversed the Mud Islands colony, the increase in intra-specific aggression that we stimulated appeared to 'spill-over' into neighbouring breeding colonies of other species, a phenomenon that has also been recorded in other colonial seabirds (Anderson and Keith 1980). Whilst highly desirable, logistically it was not feasible for us to measure the direct impact of tourist traffic on reproductive success. Success would have had to be measured non-invasively by observation from the boardwalk, which would have been very time-consuming and possibly somewhat inaccurate for birds nesting well away from the boardwalk.

Management dilemma

This study showed that although Silver Gulls in a colony that has been exposed to consistently heavy tourist traffic for 30 years were more tolerant of such disturbance than conspecifics in an isolated colony, they nonetheless responded to it behaviourally in several ways that probably had negative fitness consequences. Although each disruption to the breeding gulls' activities was relatively brief, large numbers of tourists visit the site as part of the Phillip Island 'tourist circuit' and therefore disruption is frequent. Restriction of tourist traffic to a fenced, elevated boardwalk has not eliminated these effects, particularly in gulls nesting close to the structure. An obvious next, but more difficult step would be to establish empirically the extent of the effect of these behavioural responses to disturbance on such variables as stress levels and reproductive success.

Our findings suggest that the critical negative elements of the tourist traffic at Point Grant were probably its volume, constancy, the size of groups and whether visitors stopped near gulls with chicks that were close to the boardwalk. Tourist traffic on the boardwalk could potentially be regulated to reduce the impact of these factors, but there would be a substantial ongoing cost to such regulation. The key issue is whether such an action would attract support and its cost be considered justifiable on biodiversity conservation grounds, when this native species is currently very abundant and regarded in some quarters as a pest. Irrespective of the resolution of this issue, our findings should have some applicability to the management of other Australasian ground-nesting, colonial seabirds whose status is less secure and contentious.

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